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LIFE HISTORY AND BIOLOGY OF FORBESTRA OLIVENCIA (BATES, 1862) (NYMPHALIDAE, ITHOMIINAE)

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ABSTRACT. Forbestra is the only mechanitine genus lacking a thorough life history description and little is known of its biology. Accordingly I describe the immature stages including first instar chaetotaxy, and provide observations on the biology of Forbestra olivencia from Garza Cocha in eastern Ecuador. Morphological characters from the early stages of Forbestra olivencia are identified that are unique to Forbestra and support the close relationship of Forbestra and Mechanitis. Forbestra olivencia was a moderately common butterfly at Garza Cocha during the sample period, far outnumbering other sympatric Forbestra. Ecological observations demonstrate similarities between F. olivencia and Mechanitis, but suggest F. olivencia is more restricted to shaded microhabitats.

Additional key words: Mechanitini, Mechanitis, chaetotaxy

INTRODUCTION

Ithomiine butterflies have played an important role in the development of mimicry theory, having been the original models of imitation described by Bates (1862). In that paper Henry Bates described Mechanitis olivencia based on wing color pattern differences being consistently different from other sympatric Mechanitis in the western Amazon basin. Forbes (1924) noted characters of the color pattern, wing venation, and male genitalia that distinguished "equicola and allies" from "polymnia and allies". Fox (1967) erected the genus Forbestra to contain "equicola and allies", including olivencia, and identified characters of the female forelegs as distinct from Mechanitis. In the 40 years since its description little has been published on the biology of species in the genus Forbestra, despite their being among the larger and more conspicuous ithomiines.

Recent systematic work on ithomiines has used characters from the early stages in phylogeny reconstruction (Brown & Freitas 1994, Motta 2003), making use of the fact that life history data are available for nearly all genera. Photographs of larvae and pupa of F. equicola (Cramer) (Brévignon 2003) and a brief description and drawing of the larva of *F. olivencia* by Drummond (1976) are all the life history information that exists for Forbestra. Moreover, Forbestra is the only genus lacking a thorough life history description in the tribe Mechanitini (Freitas & Brown 2002), a group comprised of several mimetic color patterns and thus of interest for the evolution of mimicry. Accordingly, I describe the early stages of Forbestra olivencia juntana (Haensch) from eastern Ecuador, and include in the descriptions characters developed for phylogeny reconstruction (Brown & Freitas 1994, Motta 2003). In addition, I report observations on the ecology, behavior and morphology of *Forbestra olivencia*.

MATERIALS AND METHODS

Observations were made intermittently between 2000-2005 at Garza Cocha (S 00°29.87', W 76°22.45'), Provincia Sucumbios, Ecuador. Early stages were reared in plastic cups and plastic bags under ambient conditions (22-30° C, 70-100% relative humidity) in a wood building with screen windows. During the drier parts of the year (December to February) larvae were moved daily from the building to a shaded environment under a nearby building to maintain ambient conditions. Observations were recorded daily and head capsules and pupal exuviae were collected. Larval specimens were boiled and subsequently stored and studied in 70% ethanol and deposited in the author's collection. First instar head capsules were treated with 10% KOH to dissociate the mandibles and labrum. Host plant vouchers were collected and deposited in the Herbario Nacional de Ecuador (voucher number: RIH-596).

Observations on adults were made at the same locality in the surrounding forest. Adults were marked and released, or collected for other studies. I recorded flight height, microhabitat conditions, and adult diet. Forewing length was measured with digital calipers and body mass was measured with a portable balance (Acculab) accurate to 1 mg. Ithomiine taxonomy follows Lamas (2004), except that *Mechanitis messenoides* Felder & Felder is treated as a species, rather than a subspecies of *M. mazaeus* Hewitson, based on observed differences in host plants, color pattern and DNA sequence data at this site (unpublished).

Results

Early Stage Biology

Host plant. Host plant specimens were compared with material in the Herbario Nacional de Ecuador and determined to be *Solanum monarchostemon* Knapp. and Michael Nec of the New York Botanical Garden confirmed the determination. *Forbestra olivencia juntana* were only found using *S. monarchostemon* at Garza Cocha. However, Elias and Willmott (pers. comm.) observed *F. olivencia* using *Solanum thelopodim* Sendtn., in addition to *S. monarchostemon*, south of the Rio Napo near Añangu.

It should be noted that the host of *F. olivencia* recorded at Limoncocha is not *Solanum anceps* Ruiz. & Pav. as reported in Drummond (1976) and Drummond & Brown (1987). The host specimen (Drummond 7315) listed in Drummond (1976) was studied by Knapp (2000) and determined to be S. *monarchostemon*.

Solanum monarchostemon was found in primary forest in well-drained, well-lit areas and associated with gaps. Individuals hosting *F. olivencia* were 0.5 - 1.3 m tall, often with flowers and/or fruits, and found in shaded areas near gaps, but not at gap edges or in gaps. A group of six *Mechanitis messenoides* eggs was found on *S. monarchostemon* and reared to be normal sized adults.

Ants were commonly found patrolling Solanum monarchostemon. Ectatomma, Crematogaster, Wasmannia, Camponotus (identified using Bolton 1994), and three unidentified genera were collected from the hosts. Crematogaster were observed attacking and carrying away *F. olivencia* eggs on one host. Ectatomma and other genera were not observed interacting with eggs or larvae, and one female *F. olivencia* oviposited on a host with Ectatomma present. In addition to ants, an unidentified species of braconid wasp was observed searching *S. monarchostemon* and larvae of a different braconid species emerged from 4th instar *F. olivencia*.

Oviposition. Eggs are laid on the upper leaf surface, but one egg was observed on the host plant main stem. Eggs were found laid singly (n=7), in pairs (n=11), and occasionally in clusters of three (n=3) or four (n=3). One group of eight eggs was also found. Host plants were commonly found with eggs on more than one leaf (9 out of 13 plants), commonly two of the larger host leaves. Eggs were found on small to large mature host leaves with little to extensive herbivore damage. As mentioned above, eggs and larvae were not found on plants in or bordering gaps.

Two oviposition events were observed at 11:00 and 14:30 respectively, and females were observed searching for hosts between 11:00 and 16:00. Females search the host very carefully for several minutes, hovering in front of leaves and main stem, inspecting both top and bottom of leaves and also descending slowly nearly to the ground while facing the main stem, then ascending to leaf height. Upon settling on a host leaf the female tests with antennae and touches her abdomen several

times to the host leaf surface. Host assessment took nearly 10 minutes for one female, and females take one to several minutes between laying each egg. Both females first laid a pair of eggs close together, then a single egg on a different leaf.

Description of early stages: Egg. Fig. 1A. Duration: 4 (n = 1) to 5 days (n = 15). Mean egg height 1.59 mm, mean width 0.87 mm, with mean axes ratio (height/width) of 1.83 (n = 3). The egg is white, taller than wide, widest in middle, tapering apically to narrow but rounded apex. Egg surface sculptured with 13-17 horizontal ridges (n = 4) and 13-15 vertical ridges (n = 4) making four-sided cells with inner corners rounded off (Fig. 1A). The four-sided cell pattern changes to pentagonal and hexagonal cells near apex.

1st instar. Fig. 1B and Fig. 2. Duration: 2 days (n = 15) to 3 days (n = 6). Mean head capsule width = 0.54 mm (n = 14). Head capsule black. Body sparsely covered with dark setae. Body is pale translucent with blue tints at either end, blue palest in posterior. Body pale laterally with yellow tints and dorsum gray to green where plant material visible. Anterior of segment T1 whitish. Rounded lateral protuberance present on abdominal segments A1-8. Dorsum traversed by subtle fleshy wrinkles. Segment A10 with dark anal plate. Thoracic legs are dark. Prolegs pale with dark patch at base and A10 proleg base darker than others. Newly hatched larvae eat one to three quarters of eggshell (n = 4) or whole eggshell (n = 3). Rest with body straight on underside of leaf along secondary or tertiary leaf veins, or near hole in leaf. Larvae sometimes eat into leaf around themselves making an isolated patch of host to rest on (see Fig. 1B).

Because characters based on first instar morphology have proven informative for ithomiine phylogeny (Brown & Freitas 1994, Motta 2003), and *Forbestra* was missing in Motta's (2003) analysis, I provide a detailed description of the first instar chaetotaxy in the Appendix. The description focuses on Motta's (2003) morphological characters so the description may be used for phylogenetic analyses. The description is based on two preserved first instars and three first instar head capsules. Arrangement and relative lengths of first instar body setae are shown in Fig. 2.

2nd instar. Fig. IC. Duration: 1 day (n = 2) to 2 days (n = 13). Mean head capsule width = 0.74 mm (n = 17). Like previous instar with the following changes. Body less translucent and pale to pale-yellow laterally. T1 is pale dorsally with blue tints, and fits snugly with posterior of head capsule. Aorta is visible dorsally. Middle body segments dorsally gray-green where food visible. Posterior to A6-7 the dorsum is pale to yellowish turning bluish on A8-9. Lateral protuberance on A3-6 rounded, those on A1-2 and A7-8 are more pointed and larger, with those on A1-2 largest. Thoracic legs and prolegs are pale with thoracic legs darker than prolegs. One individual. Commonly rest on leaf underside with body straight, lying along a secondary vein with head away from leaf midvein.

3rd instar. Fig. 1D. Duration: 2 days (n = 11). Mean head capsule width = 1.06 mm (n = 12). Like previous instar with the following changes. Thorax dorsum nearly white in anterior of T1 turning blue in posterior T1, then fades to gray in T3. Thorax is white laterally. Rest of body grayish dorsally, turning blue again on A8-9. Segment A10 white dorsally and laterally. Lateral abdominal protuberances yellowish in color, except for on A8, which is white. Lateral protuberances are rounded triangles with A1-2 longest and thinner than rest. Ventrally pale translucent. Rest on underside of leaf on midvein with body straight. When disturbed raise head and thorax off leaf substrate maintaining straight posture.

4th instar. Fig. 1E. Duration: 2 days (n = 11). Mean head capsule width = 1.44 mm (n = 9). Like previous instar with the following changes. A pair of small dorsal humps present on T1. T1-2 blue dorsally and laterally. Anterior of T3 faint blue dorsally, fading to light gray. T3 pale yellow laterally. A1-7 yellowish gray dorsally. A8-10 blue dorsally, with A10's posterior fading to pale. Lateral protuberance on A1-2 tapering to thin fleshy projection about twice as long as those on A3-A8. A3's lateral protuberance longest of A3-6 but shorter than A7-8. A1-7 lateral abdominal protuberances yellowish,

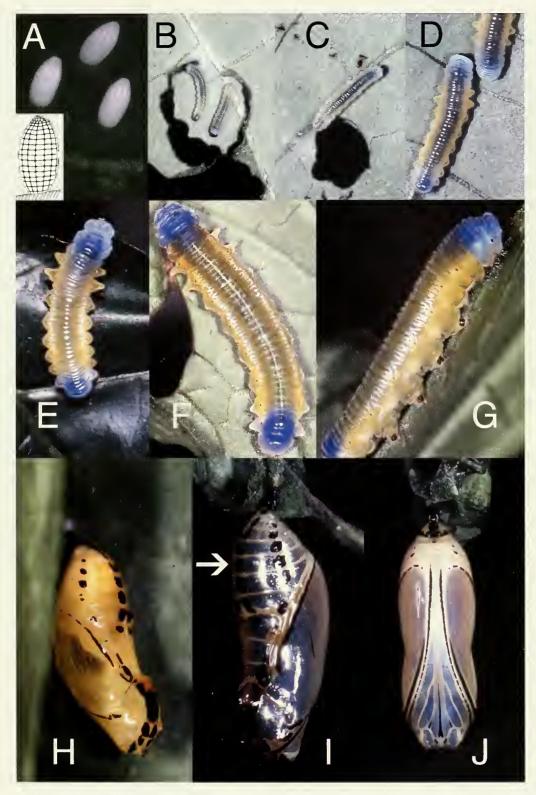


FIGURE 1. Forbestra olivencia life history. A. Leaf-top cluster of 3 eggs (image is a composite of two photos of same clutch of eggs), inset is egg drawn from specimen after storage in 70 % ethanol. B. First instar. C. Second instar. D. Third instar. E. Fourth instar. F. Fifth instar. G. Lateral view of fifth instar showing dark thoracic legs and dark patches on prolegs 3-6. H. Pupa with first day coloration. I. & J. Final pupa coloration in dorsolateral (I) and ventral view (J).

vellow strongest on A1-2 and A6-7. A8's lateral protuberance is pale. White stripe present on dorsal midline of abdomen. White dorsolateral stripe present above abdominal protuberance on segments A3-6, then fading on A7. Rest on leaf underside with head down and body straight. At rest, head capsule partly obscured in dorsal view by T1. Feed from leaf margin near its apex. Braconid wasp larvae emerged from 4th instars and resulted in larval mortality.

5th instar. Fig. 1F and G. Duration: 4 days (n = 7) to 5 days (n = 3). Mean head capsule width = 2.00 mm (n = 4). Like previous instar with the following changes. Head capsule black with pale pubescence, sutures visible as light lines, and labrum light gray. T1's dorsal fleshy humps more pronounced. T1-2 blue dorsally and laterally. T3 dorsally darker than T1-2, and pale yellow laterally. A7 posterior is blue dorsally. Dorsum of A8-9 blue, but A10's whitish. Abdomen segments A1-7 yellow laterally including lateral abdominal protuberances, yellow extending onto dorsum. AS-A10 pale laterally. White dorso-lateral stripe above lateral protuberance starting in posterior of A2 and ending in anterior of A7 (mainly on A3-6). Lateral protuberances of A1-2 and A7 with white tips. Lateral protuberance of A3-8 triangular to broadly triangular. Protuberance on A1-2 twice the length of those on A4-6. A3, A7, and A8 with slightly longer more pointed protuberances than those of A4-6. Spiracles obvious and dark on T1, A1-8. Dorsum with central white to yellowish line over aorta from posterior T3 to A7. Aorta visible dorsally, and appears pale T3-A7 and dark on T2 and A8-9. Thoracic legs are black. Prolegs have dark gray to black sclerotized plate near base, this not strongly sclerotized on A6 and A10 in some individuals. Prolegs with pale pubescence near base. Pale translucent ventrally with tracheae visible. Day before pupation body turns very yellow and blue of body fades. When disturbed tuck head capsule under T1, totally obscuring head capsule dorsally. Rest head down on underside of leaf with head near where eating at margin. Larvae in groups of 2-4 stay together in all instars and no cannibalism was observed.

Pupa. Fig. 1H, I and J. Duration: 8 days (n = 9). Reflective metallic, elongate and pendant. At first all yellow without any black markings other than cremaster. Within first 24 hours black marks develop on yellow pupa (Fig. 1H) followed by yellow turning to silver with gold highlights (Fig. 1I and 1J). Cremaster black. Ventral black line extending from cremaster to region between segments AS and A9 with pair of bumps, and there expanding laterally, overall making an anchor-shaped patch. Anterior to anchor-shaped patch, ventral abdominal midline with small faint black spots that are absent in some individuals. Ventro-laterally, abdomen has pair of black flecks on segments A5-6, segment A6's smaller. Spiracles outlined in large squarish black spots on segments A3-8, decreasing in size toward cremaster. Abdomen dorsum with series of eight squarish black spots

that are separated into pairs on segments A2, A8, A9, partially fused on segments A3 and A7 and completely fused forming one large spot on segments A4-6 (arrow in Fig. 11). A few individuals had dorsal black spots incompletely fused on A6. Together this pattern makes an elongate narrow "X", with arms of "X" more widely separated at anterior end. In between dorsal abdominal segments colored orangebrown. Transverse ridge present in anterior of A3 making a small sheft. Antennae edged in black line that is broken into dashes in middle third only. Wing pad edged black ventrally fading completely after mid-length. Wing pad edged brown and black dorsally turning to dashed black line and ending near apex. Wing pad marked only with thin black line near center. Thorax weakly keeled. Thoracic dorsum colored with broad black stripe that splits around a brown patch in posterior. Anterior to black squares located at base of antennae, and black triangles present on slightly pointed ocular caps. The day before eclosion bluish tints develop, then wing pad margin develops distinct black before the wing colors finally show through.

Adult Biology: In 204 days of fieldwork at Garza Cocha between July-August 2000, May-July 2001, May-July 2002, January-February 2003 and December 2004-January 2005, 83 individuals of F. olivencia were seen (recaptures excluded), 68 of which were captured and sexed (21 males, 47 females). F. olivencia ranked 13th in abundance out of 56 ithomiine species in the overall rank-abundance distribution of capture data during this period. F. olivencia was much more common than Forbestra equicola during the study period (F. equicola ranked 40th with 6 individuals), and a single F. proceris (Weymer) was captured outside the study period in June 2005. With respect to other mechanitines, F. olivencia tied Mechanitis mazaeus in abundance and was more common than other Mechanitis. F. olivencia was less common than Scada zibia (Hewitson) (11th in rank abundance with 99 individuals) and more common than Thuridia psidii (Linnaeus) (46th in rank abundance with two individuals). Among ithomiines with similar mimetic 'tiger' coloration (Beccaloni 1997), F. olivencia was the third most abundant species.

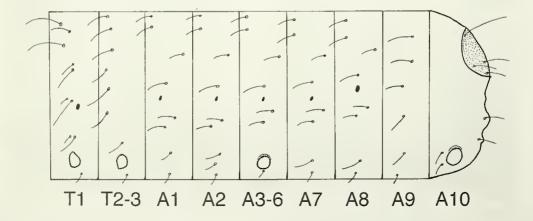


FIGURE 2. First instar body chaetotaxy. Setae drawn to represent relative lengths.

Forbestra olivencia was lowest in abundance in July-August 2000 with only four individuals (0.11 individuals per day) and more common in other sampling periods with 13 individuals during May-July 2001 (0.23 individuals per day), 25 individuals during May-July 2002 (0.47 individuals per day), 19 individuals during January-February 2003 (0.76 individuals per day), and 22 individuals during December 2004-January 2005 (0.62 individuals per day).

Forbestra olivencia inhabits primary forest. Females are commonly seen flying in the understory with a mean flight height above the ground of 1.0 m (n = 39, s.d. = 0.63). Males were observed flying higher than females at a mean height of 1.6 m (n = 20, s.d. = 0.86; unpaired t-test, t = -2.7, P = 0.009). Individuals were observed only in shaded forest or near small forest gaps. Although no individuals of *F. olivencia* were observed in open areas, *F. proceris* was observed visiting Asteraceae flowers in a cleared field.

Observed adult resources of *F. olivencia* at Garza Cocha include bird droppings, and rarely splattered fruit or other leaftop detritus. *F. olivencia* females visit bird droppings (n = 5; Fig. 3A), and were observed flying in the immediate vicinity of army ants (*Eciton* spp.) stopping at white fungal patches on leaves and bird droppings. One male was observed feeding on bird droppings. No *F. olivencia* were observed visiting Asteraceae flowers or other pyrrolizidine alkaloid sources during this study.

F. olivencia is sexually dimorphic with respect to size. Forewing length of wild-caught females (mean = 33.88mm, s.d. = 2.30 mm, N = 27) is significantly longer than wild-caught males (mean = 31.97 mm, s.d. = 2.64 mm, N = 14; unpaired *t*-test, t = 2.40, P = 0.021). However female body mass (mean = 72 mg, s.d. = 19 mg, N = 20) is not significantly higher than males (mean = 65 mg, s.d. = 21 mg, N = 11; unpaired *t*-test, t = 0.99, P = 0.3). Mating takes place during the middle of the day as a pair was seen in copula at 13:00 with the smaller individual, presumably male, flying. Forewing length of reared females (mean = 32.80, s.d. = 0.85, n = 4) and males (mean = 31.33, s.d. = 1.88, n = 4) did not differ from wild-caught individuals of the same sex (unpaired *t*-test, t = 0.91, P = 0.37 for females, and t = 0.45, P = 0.66 for males).

DISCUSSION

The genus *Forbestra* ranges throughout the Amazon basin and Lamas (2004) recognizes three species (*F. equicola, olivencia, and proceris*). *Forbestra* species participate in "tiger" mimicry complexes with other ithomiines and heliconiines (Beccaloni 1997, Brown 1988). These species exhibit a combination of orange





FIGURE 3. Adult *F. olivencia juntana*. **A**. Ventral wing pattern of female feeding on bird dropping. **B**. Dorsal wing pattern of male reared from larva.

hind wing with transverse black bar, and forewing with orange, yellow and black oblique stripes (Fig. 2).

Morphology of *Forbestra olivencia* early stages provides useful characters to identify *F. olivencia*, and corroborates both the generic status of *Forbestra* and the sister relationship between *Mechanitis* and *Forbestra*. Characters of first instar chaetotaxy developed for phylogenetic analysis described in this study (Appendix) are not discussed further. In addition to *F. olivencia*, data for *Sais rosalia* were lacking from Motta's (2003) analysis, and were not included in Freitas and Brown's (2002) description of *Sais rosalia* early stages. Thus comparison of first instar chaetotaxy for all genera of Mechanitini was not undertaken here. Two characters of *F. olivencia* early stages appear mique to this species. First, the pupa has dorsal black abdominal spots that make a narrow "X" and completely merge only on A4 - 6 (arrow in Fig. 11). *F. equicola*'s black abdominal spots merge on A4 - 8 and no data on the immatures of *F. proceris* are yet available. Second, *F. olivencia* larvae have elongate lateral protuberances on A1-2 reminiscent of those along the abdomen of *Mechanitis*. Such protuberances are not present on *F. equicola* (Brévignon 2003). However, these elongate lateral protuberances may be variable as Drummond's (1976) larval drawing of *Forbestra olivencia juntana* (called *F. truncata juntana*) from Linnoncocha lacks elongate protuberances on A1-2.

Like Mechanitis, F. olivencia lays eggs on leaf tops. However, F. olivencia typically lays eggs singly or in small clusters of 2 - 4 and not large clusters as in Mechanitis. Although there is no information on F. equicola egg clutch size in Brévignon (2003), the fact that the larvae are together on a single leaf suggests equicola also lays eggs in groups of small size (~ 6). Thus the genus Forbestra appears to lay eggs in smaller clutches than Mechanitis and additional observations on Forbestra species would clarify whether there are consistent differences between these genera.

The pupa of Forbestra olivencia is strikingly similar to Mechanitis messenoides and M. mazaeus at Garza Cocha (unpublished). F. olivencia pupae differ from those of Mechanitis primarily in the arrangement of the rows of black dorsal abdomen spots. In F. olivencia these spots completely join on segments A4 - 6 making an "X" (arrow in Fig. 11), and in F equicola they are fused on A4 - 8 and separated on A2-3. In M. messenoides and M. mazaeus (and M. polymnia Fox 1967, Fig. 7) the spots come close together on segments A4 - A6 but do not join and other mechanitine genera have them located more subdorsally (Brown & Freitas 1994, Fig. 4F and A. Freitas pers. comm.). Thus, in addition to genitalia, wing and leg characters (Forbes 1924 and Fox 1967), the dorsal fusion of these spots on A4 - 6 is likely a synapomorphy for Forbestra.

The close relationship between *Forbestra* and *Mechanitis* recognized by Bates (1862), Forbes (1924), and Fox (1967) is supported by characters of the immature stages (Brown & Freitas 1994, Fig. 1A) as well as DNA sequence data (Brower et al. 2006). Synapomorphies from the immature stages (excluding 1st instar chaetotaxy) supporting this relationship identified by Freitas and Brown (1994) and corroborated here include: egg axes ratio > 1.7, eggs laid on upper side of leaf, and laying eggs in groups. In addition, two other characters identified in this study support this relationship: larva with a pair of short dorsal

fleshy humps on T1 (albeit *Forbestra olivencia*'s are shorter and more rounded than in *Mechanitis*), and in the pupa the dorsal abdominal spots lie near the dorsal midline.

The sister relationship of *Forbestra* and *Mechanitis* implies similarities in ecology and behavior between these genera. Observations on *F. olivencia* at Garza Cocha largely support this. For example, the single observation of *Mechanitis messenoides* using *F. olivencia*'s host suggests similar tolerances to host plant chemistry. Furthermore, *F. olivencia* feed on bird droppings and follow army ants similar to *Mechanitis* (Ray & Andrews 1980). Though the data are few (five females and one male were observed feeding on bird droppings), they show a female bias in feeding on bird droppings as documented for *Mechanitis* and *Melinaea* (Ray & Andrews 1980).

Males of ithomiine species avidly visit Asteraceae and Boraginaceae flowers and plant parts to gather pyrrolizidine alkaloids (Brown 1984a, 1984b, 1987, Brown et al. 1991, Pliske 1974, 1975). Mechanitis are commonly seen feeding on Asteraceae in gaps, secondary growth and cleared areas at Garza Cocha. Despite equal effort sampling all species of ithomiines and making observations in the early morning at flowers fed on by other ithomiine species, F. olivencia was not observed feeding on flowers during this study. This almost certainly does not reflect a difference between F. olivencia and Mechanitis and instead is attributed to chance. A male Forbestra proceris was found feeding on Asteraceae in an open habitat in the early morning. Furthermore A. Freitas has observed F. olivencia males visiting Asteraceae in the early morning in Brazil (pers. comm.).

There does seem to be a microhabitat difference related to host plant use between *F. olivencia* and *Mechanitis* species at this site. *F. olivencia* adults were not observed in open areas or in forest gaps. *Solanum monarchostemon* was found in and around gaps, and in well-lit areas of forest. *F. olivencia* eggs and larvae were not found on hosts in gaps or in sunny areas at gap edges. In contrast, *Mechanitis* eggs and larvae are commonly found on their host plants in gaps and open areas, and *Mechanitis* are more commonly seen flying in gaps and very open areas at this site. Differential microhabitat use by *F. olivencia* relative to *Mechanitis* deserves further investigation as it pertains to a correlation between microhabitat and mimicry (DeVries et al. 1999, Mallet & Gilbert 1995).

Despite the observation that specimens of *Forbestra* are uncommon in natural history collections (Fox 1967), *F. olivencia* was moderately common at Garza Cocha during this study ranking as the 13th most abundant

ithomiine. F. olivencia was highest in abundance in the drier months sampled (December to February) with 0.76 individuals per day in January-February 2003 and 0.62 individuals per day in December 2004 to January 2005. During the wetter months of May-August F. olivencia varied in abundance year to year (0.11, 0.23 and 0.47 individuals per day in 2000, 2001, 2002, mean = 0.27) but did not exhibit extreme fluctuations in abundance during the study period. Although all three Forbestra species have been observed at Garza Cocha they are not equal in abundance. Forbestra olivencia was much more common than both *F. equicola* and *F.* proceris. Ithomiines are numerically dominant members of neotropical mimetic butterfly assemblages (Beccaloni 1997, Brown & Benson 1974) and observations at Garza Cocha confirm this (unpublished). F. olivencia is likely an important component of the mimetic community at this site, being tied for the third most abundant ithomiine species of the 13 that share its mimetic color pattern.

Observations on parasitoids, predators and host abundance provide potential explanations for moderate population density of *F. olivencia* at this site and time period. Larval parasites were found in low abundance during rearing. Adults probably suffer mortality from avian predators as beak marks were found on the wings of some individuals. As mentioned above, ants in the genus Crematogaster attack eggs and are commonly seen patrolling the host plants. Thus, Crematogaster could play a role in population dynamics of F. olivencia. Given the careful searching by the female during oviposition it seems probable that females are checking for presence of ants, or assessing presence of conspecific eggs and larvae. The host of F. olivencia at Garza Cocha is not uncommon, but does not approach the high abundance of hosts of more common ithomiines at the site. Detailed study of these factors could contribute to the understanding of population dynamics in this species.

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APPENDIX: FIRST INSTAR CHAETOTAXY

In the description of first instar chaetotaxy that follows numbers in parentheses correspond to characters in Motta's (2003) Table 19.2. Setal nomenclature follows Motta (2003). Hinton (1946), Kitching (1984) and Peterson (1962) were also consulted. Descriptions are given here rather than a table of character states because of perceived ambiguity or difficulty interpreting some of the characters. In the following descriptions T1, 2, 3 are pro-, meso- and metathoracic segments respectively, A1-10 are abdominal segments, and unless otherwise noted setal characters apply to all segments where present.

Ccphalic capsule. Seta C1 equidistant to frontal and anteclypeal sutures (1). Seta C2 nearer to C1 than to a medial imaginary line (2). Seta C2 same length at C1 (3). Seta F1 undoubtedly more dorsal and medial to C2 (4). Seta F1 nearer to C2 than it is to coronal bifurcation (5). Seta F2 equidistant or subtly nearer to frontal suture than to imaginary medial line (6). Puncture Fa clearly above seta F1 (7). Distance between Fa punctures similar to that between Fa and F1 (S). Puncture AFa, and setae AF1 and AF2 all present (9). Puncture AFa medial to line connecting setae AF1 and AF2, forming obtuse triangle with angle between AFa and AF1/AF2 ~160° (10). Puncture AFa closer to seta AF2 relative to AF1 (11). Setae AF1 and AF2 similar in length (12). Seta AF2 subtly above level of coronal suture bifurcation (13). Distance of seta AF2 to coronal suture same as distance of AF1 to frontal suture (14). Puncture Aa above line connecting AF1 and A2 (15). Puncture Aa nearer to A2 than to AF1 (16). Seta A3 just posterior to imaginary line between stemma iv and P1; distance of A3 to the imaginary line less than distance of A3 to stemma iv (17). Seta A1 closer to stemma i than ii and aligned to slightly above stemma i (1S). Seta A2 aligned with imaginary line between stemma ii and AF1 (19). Seta A3 longer in length than A2 and L1 (20). Puncture Pa ventral to imaginary line connecting setae A2 and A3 (21). Puncture Pa nearer to seta A2 than to A3 (22). Puncture Pb medial to imaginary line between setae P1 and P2 (23). Puncture Pb closer to seta P2 than P1 (24). Seta P1 farther from coronal suture than is seta P2 (25). Seta P1 twice as long as length of P2 (26). Relative distance of puncture La to seta L1, 1/3 distance between L1 and A3 (27). Alignment of puncture La and setae L1 and A3 forming a triangle (28). Seta O1 nearly in line with i and iv, equidistant to iii and iv; distance of O1 farther to iii than ii (29). Angle formed between O2 and stemmata iv and v slightly less than 90° (30). Seta O2 equidistant to stemmata iv and v (31). Seta O2 longer than O1 and O3, with O1 and O3 similar lengths (32, 33). Seta O3 aligned to slightly ventral than stemma v and groove (34). Puncture Oa nearly aligned with stemma i and seta A1 and very near stemma i (35). Puncture Ob forming an angle between stemma v and O2 (36). Puncture Ob equidistant to v and O2 (37). SO1 in ventral end of antennal socket so that distance of SO1 to end of antennal socket is less than 1/2 distance between SO1 and SO3 (3S). SO2 subtly ventral to stemmata v and vi (39). SO2 equidistant to v and vi (40). SO3 posterior to line between stemma vi and SO1 (41). SOa aligned to slightly nearer to suture relative to line between SO3 and C1 (42). SOa falls on line between SO2 and nearest point of maxillary (ventral) suture, SOa is closer to SO3 than to the suture and closer to the suture than to SO2 (43). SOb very near to the antennal socket (44). Relative distance of SOb to stemma vi and SO3 varies from nearer to stemma vi to equidistant (45). G1 closer to groove

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than to maxillary (ventral) suture (46). Ca ventral to line joining G1 and O3 (47). Ga slightly nearer to equidistant to C1 relative to O3 (4S). V1 equidistant between P2 and "V" group (49). Stemmata all similar diameter (50). Distance from stemma iii to iv shorter than from i to ii, and ii to iii (51). Stemma v equidistant to iv and vi (52).

Mandible and labrum. Seta M2 aligned between L1 and L2 or aligned with L1 (53). Seta M2 subtly ventral to line between M1 and L2 (54). Seta M1 shifted dorsally relative to M2 (55). Distance between M1 setae equivalent to distance between M1 and M2 setae (56). Seta M2 about twice as long as M1 (57). Puncture S (called "S' in Motta 2003, called "P" in Peterson 1962) located nearer to the basal suture or posterior border relative to M1 and M2 (58, 61). Puncture S located dorsally and nearly in line vertically with M2 such that a line connecting the two would be nearly parallel to imaginary midline (59). Mean angle of lines connecting M1, M2 and puncture S 40 - 70° (60). Puncture S in line vertically with longest part of labrum (labral lobe) and very dorsal of widest part of labrum (between L1's) (62). Seta M3 on distal border of labrum (63). Seta L2 much nearer to L1 than to L3 (64). Seta L1 very slightly distal to widest part of labrum (65). Less sclerotized region of labrum spans notch to just before M3 (66). Less sclerotized basal patches absent (67). Internal border of labral lobe smoothly curved (68). Labral notch angle obtuse (69). Ratio of notch length (= depth) to overall labral length (labral lobe to base) -0.8; ratio of notch width, as measured between M3's, to labral length ~ 0.5 (70). Ratio of labrum width (between L1's) to length (labral lobe to base) ~ 2 (71). More than three small molar teeth (72). Incisors 2 and 3 similar lengths (73). Lateral grooves radiating from each side of 4th incisor, 4 grooves in total (74).

Body. No tubercles present on the thorax (75). Average seta length is less than segment width except for the longer XD1 and XD2 setae on T1 which are nearly as long as segment width (77). Crochets arranged in a circle pattern (78) with inner and outer crochets similar length (79). Prolegs with more that 14 crochets on average (80). Cervical sclerite absent on XD1 and XD2 and D1 (81). Seta D1 shorter than XD1 and XD2 which are equivalent in length (S2). Setae SD2 and SD1 aligned on T1, SD2 shifted slightly posterior to SD1 on T2 and T3, and SD2 shifted very posterior to SD1 on abdomen (83, 87). On segment T1 setae L1 and L2 slightly dorsal of spiracle with L2 between L1 and spiracle (84). Setae D1 and D2 are equivalent lengths (S5, 91). Seta SD2 closer to SD1 on thorax but equidistant to SD1 and D2 on abdomen (86). Seta SD2 ventral and aligned with D1 and D2 on thorax but ventral and posterior to D1 and D2 on abdomen (8S). Seta SD1 longer than L1 and equivalent to L2 on T1; SD1 equivalent to L1 and L2 on T2/3 and abdomen (S9, 94). Seta L2 present on segments T1-A8 (90). Seta SD2 longer than D1 and D2 on T2/3, SD2 and D1/2 similar lengths on other segments (92). SD1 longer than SD2 on T1, SD1 slightly shorter than SD2 and equivalent to D1/2 on T2/3, and SD1 equivalent to slightly longer than SD2 on abdomen (93). Seta L2 longer than L1 on T1 and equivalent to slightly longer than L1 on other segments (95). Additional SV seta present only on T1 and A2 (96). Segment A9 relative to A7/8 missing two setae (one of L1/2 and one of SD1/2 (97). On segment A10 seta D1 longest, SD1 and L1 equivalent and D2 shortest (98). Setae P1 and SPI both present on segment A10 (99).